# Thermoregulation, Heart Rate and Water Balance in the Fennec Fennecus zerda (Zimm.)

**DISSERTATION**

zur Erlangung des Grades eines
Doktors der Naturwissenschaften
dem Fachbereich Biologie
der Eberhard-Karls-Universität zu Tübingen

vorgelegt von

Ursel Noll-Banholzer
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Dekan Prof. Dr. K.P. Hadeler
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# THERMOREGULATION, HEART RATE AND WATER BALANCE IN THE FENNEC FENNECUS ZERDA (ZIMM.)

Part I : BODY TEMPERATURE, OXYGEN CONSUMPTION, EVAPORATIVE WATER LOSS AND HEART RATE IN THE FENNEC

Part II: WATER BALANCE AND KIDNEY STRUCTURE IN THE FENNEC

Fennec with ECG transmitter assembly

# THERMOREGULATION, HEART RATE AND WATER BALANCE IN THE FENNEC FENNECUS ZERDA (ZIMM.)

## Part I: BODY TEMPERATURE, OXYGEN CONSUMPTION, EVAPORATIVE WATER LOSS AND HEART RATE IN THE FENNEC

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## ABSTRACT

1. The daily course of heart rate and body temperature in fennecs resembles that of nocturnal mammals. Overall heart rate is 130 $min^{-1}$, average body temperature amounts to 38.1 °C.

2. Body temperature is maintained constant at ambient temperatures between 10 °C and 32 °C but rises sharply with higher $T_a$.

3. Fennecs have a wide thermoneutral zone which extends from 23.4 °C to 32.0 °C.

4. Basal metabolic rate (0.358 ml/g h) is only 60.7 % of the value predicted on the basis of body mass. Minimal conductance is 23 % below the expected level; thus fennecs are also well adapted to low ambient temperatures.

5. At low and moderate ambient temperatures fennecs have a low rate of evaporative water loss. At a $T_a$ of 38 °C, only about 56 % (maximum 75 %) of the metabolic heat are lost by evaporation.

6. Basal heart rate is considerably reduced. Oxygen pulse increases with decreasing ambient temperature. The higher oxygen demands below thermal neutrality, however, are met primarily by a rise in heart rate. During rest, fennecs show a marked arrhythmia of the heart rate.

7. Body temperature of newborn fennecs is about 6.3 degrees below the adult level. The young show a metabolic response to cold from the first day of life, but they are not yet able to maintain their $T_b$ at a constant level when exposed to a $T_a$ of 16 °C.

## INTRODUCTION

Up to now there is only little information available on the metabolic responses of wild carnivorous mammals in arid environment. Kennedy & Macfarlane (1971) studied the mulgara (Dasycercus cristicauda), a carnivorous marsupial which is desert-adapted and has a low rate of oxygen consumption, whereas the grasshopper mouse (Onychomys torridus), a carnivorous rodent, shows no reduction in basal metabolic rate and has a high pulmocutaneous water loss (Whitford & Conley, 1971). Referring additionally to the investigations of Schmidt-Nielsen & Haines (1964) on the water balance, the authors state that grasshopper mice possess no special physiological adaptations for desert life.

The present study on the fennec (Fennecus zerda) which lives in the Sahara was performed to provide some information on the metabolic and cardiovascular responses of a true carnivore to the desert environment.

**Acknowledgement**

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## MATERIALS AND METHODS

### Animals and Maintenance

On the whole eight fennecs, three males and five females, were used in this study. In 1974, the Zoological Garden in Stuttgart, W.-Germany, kindly consigned us a female, and a male was picked up from a dealer. The remaining six animals were captured in the region of the Chott El Djerid, South Tunisia, in the years 1974 and 1976. The free-ranging animals were kept in groups in two rooms (4.7 x 2.5 x 2.5 $m^3$ and 4.7 x 1.2 x 2.9 $m^3$, respectively) at an ambient temperature of 25 ± 1 °C and a relative humidity of 50 ± 5 % under a photoperiod of 12 L : 12 D (500 lx : 0.03 lx; 8.30 - 20.30). The ground of both rooms was sanded at a depth of 5 to 10 cm. Two wooden boxes in each room served as hiding-places. Book-shelves and a table were accepted for climbing. The animals adjusted well to captivity, and few of them even got tame. They were mainly fed white mice, chicken and bananas, supplemented by vitamines. Rolled oats, dates, apples, mealworms, grasshoppers and baby food were offered occasionally. Water was provided ad libitum.

### Oxygen Consumption and Carbon Dioxide Production

Oxygen uptake was determined in an open flow system either with a Hartmann & Braun Oxytest S (Frankfurt, W.-Germany) or with a Beckman paramagnetic oxygen analyzer model G 2 (Fullerton, California). During most runs, $CO_2$ production was measured simultaneously by means of a Hartmann & Braun Uras MT. Air flow (60 l/h and 80 l/h, respectively) was controlled with flowmeters (Rota, Oeflingen-Säckingen, W.-Germany) and corrected to STP. The error arising by neglecting the difference in volume between inspired $O_2$ and expired $CO_2$ is small and was not taken into account. To remove the water vapour produced by the animal, air from the respirometer chamber was passed through cylinders containing fine-mesh calcium chloride. The animal chamber consisted of a perspex box (39 x 25 x 28 $cm^3$) one side of which was transparent to allow an observation of the experimental animal. The ambient temperature ($T_a$) inside the respirometer chamber was controlled to the nearest 0.5 °C of the desired level by placing the box in a constant-temperature cabinet. Resting metabolic rate (RMR) was determined on post-absorptive animals during exposures of respectively 4 to 6 hours to ambient temperatures ranging from 10 °C to 36 °C. To minimize the influence of circadian rhythms all measurements were made at the same time of day during the animals' resting period (lights on). Subsequently to a training period of about three weeks prior to measurements, the fennecs fell asleep shortly after being placed in the metabolic chamber. They could adjust to a given $T_a$ for at least 2.5 hours after which oxygen uptake and carbon dioxide production were averaged from the lowest readings which remained constant for at least 30 minutes.

## Body Temperature

Body temperature ($T_b$) was measured rectally at a depth of 21 mm to within 0.2 °C by use of an electronic thermometer (Ahlborn, model 4448-1, Holzkirchen, W.-Germany). The relation of $T_b$ to different ambient temperatures was studied in connection with the oxygen uptake measurements. $T_b$ was taken within the first minute after removing the animal from the respirometer chamber. To examine the diurnal rectal temperature, no more than 3 measurements per day were made within the same group of fennecs.

## Heart Rate

Heart rate (HR) was obtained telemetrically by means of an ECG transmitter according to Mackay (1970). The transmitter assembly inclusively batteries and electrodes weighed 27.9 g. It was covered by a leather bag to prevent the fennecs from chewing on it, and was attached on the animals' back with two elastics stretched round the body. Two surgical clips, one fixed on a shoulder and the other in the opposite position on the back, furnished excellent contact. After an adjustment of about 6 days, the fennecs tolerated the transmitter unit, they showed no signs of unusual strain and moved freely within their group as before. The ECG signals were received by a commercial radio set and then uniformed by the trigger of an oscilloscope (Philips PW 3330/3347, Eindhoven, Netherlands). By variations in the time base of the oscilloscope it was possible to delay the signals. Thus jamming could be cleared off. Applying a preset time of 1 minute, the uniformed signals (x-deflection voltage of the oscilloscope) were adapted to the Philips scaler/timer PW 4230/4260 by use of the Stimulator T (Sachs, Hugstetten-Freiburg, W.-Germany). To show the ECG pattern, heart beats of some tests were graphed with a recorder (Metrawatt, Servogor 2s, Nürnberg, W.-Germany). Resting heart rate (RHR) at various ambient temperatures was determined simultaneously to the oxygen consumption measurements. The diurnal cycle of heart rate was studied in fennecs living within their group in a semi-soundproof room. In this case, signals were recorded over 10 minute-periods at hourly intervals and, in addition, at the changing of the lights at 8.30 and 20.30, respectively.

## Evaporative Water Loss

Evaporative water loss (EWL) in relation to $T_a$ was calculated on the basis of body mass loss ($\Delta M$) corrected for the respiratory exchanges according to the formula
$EWL\ (g/h) = \Delta M\ (g/h) + O_2\ (g/h) - CO_2\ (g/h)$; Chew (1951).
This equation may be converted to
$EWL\ (g/h) = \Delta M\ (g/h) - (V_{O_2} / 22.4)\ (44\ RQ - 32)\ (g/h)$, where $V_{O_2}$ denotes the oxygen uptake in l/h and RQ is the respiratory quotient. In each run, oxygen consumption and $CO_2$ production were measured directly. Tests were used only if the animals neither urinated nor defecated.

If not indicated otherwise, all data are mean ± standard error (SE).

# RESULTS

## METABOLIC ADAPTATIONS

### 1.1 Diurnal Body Temperature

Diurnal body temperature was determined in six animals which were fed at irregular times. Fennecs show a marked circadian cycle of body temperature in phase with the photoperiod (Fig. 1). The maximum mean of 38.7 °C is reached at 21.00 after the lights are turned off. At night when the animals are active, $T_b$ varies about 38.5 °C (range: 37.4 °C - 39.5 °C).

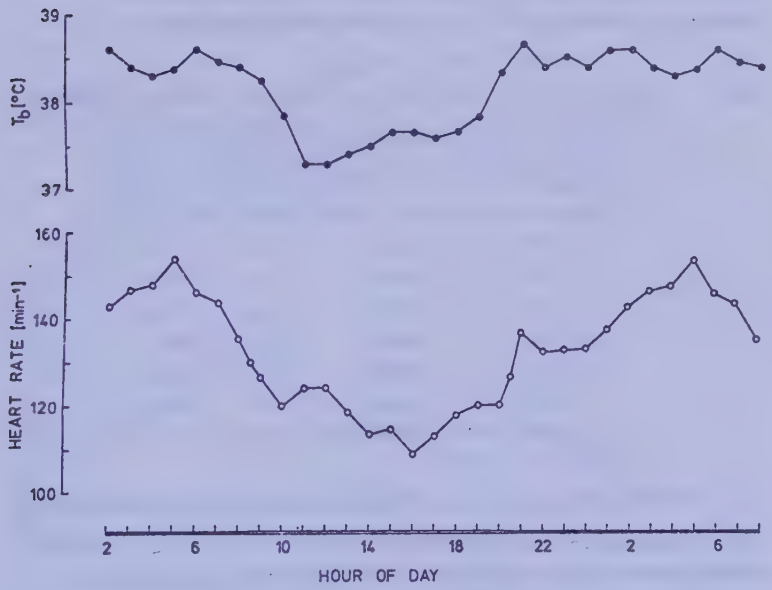


Fig. 1 Diurnal variations of body temperature and heart rate in fennecs kept under a timed light cycle of 12L : 12D (500 lx : 0.03 lx; 8.30 - 20.30).
Body temperature (solid circles) was taken rectally in 6 animals; 0.08 °C $\leq$ SE $\leq$ 0.18 °C.
Heart rate (open circles) of 4 fennecs was measured by telemetry for altogether 80 days; 2.4 $min^{-1} \leq SE \leq 3.2\ min^{-1}$.

With beginning daytime, $T_b$ drops within the first two hours to a minimum of 37.3 °C, and then rises gradually to about 37.6 °C. The mean $T_b$ in the resting period is 37.7 ± 0.05 °C, the average rectal temperature all day long amounts to 38.1 ± 0.04 °C (250 measurements).

### 1.2 Body Temperature at Different Ambient Temperatures

When subjected to ambient temperatures between 10 °C and 32 °C for 4 to 6 hours, rectal temperature remains fairly constant at a mean of 37.5 ± 0.07 °C (Fig. 2). Above thermal neutrality $T_b$ increases up to 39.5 ± 0.4 °C at a $T_a$ of 38 °C. The response of $T_b$ to high ambient temperatures differs individually (Table 1). At about 35 °C the animals start panting.

Table 1 Maximum body temperatures of fennecs at high ambient temperatures

| $T_a$ (°C) | Exposure time | Sex | $T_b$ (°C) |
|---|---|---|---|
| 38 | 2h 15' | ♀ | 41.6 |
| 35 | 1h 30' | ♀ | 40.5 |
| 36 | 4h 15' | ♀ | 40.3 |
| 36 | 5h 25' | ♀ | 40.3 |
| 36 | 3h 45' | ♂ | 41.9 |
| 38 | 3h 20' | ♂ | 40.2 |

### 1.3 Resting Metabolic Rate, Thermoneutral Zone and Conductance

Fig. 3 represents the metabolic response of 5 fennecs to ambient temperatures between 10 °C and 36 °C. The thermoneutral zone is relatively large extending from 23.4 °C to 32 °C. The basal metabolic rate (BMR) of 0.358 ml/g h ± 0.003 was derived from 82 measurements (mean body mass M = 1,106 ± 24 g). Below 24 °C the increase of oxygen consumption with decreasing $T_a$ is described by the equation RMR (ml/g h) = 0.897 - 0.023 $T_a$ (°C) (correlation coefficient r = 0.992), obtained by the method of least squares.

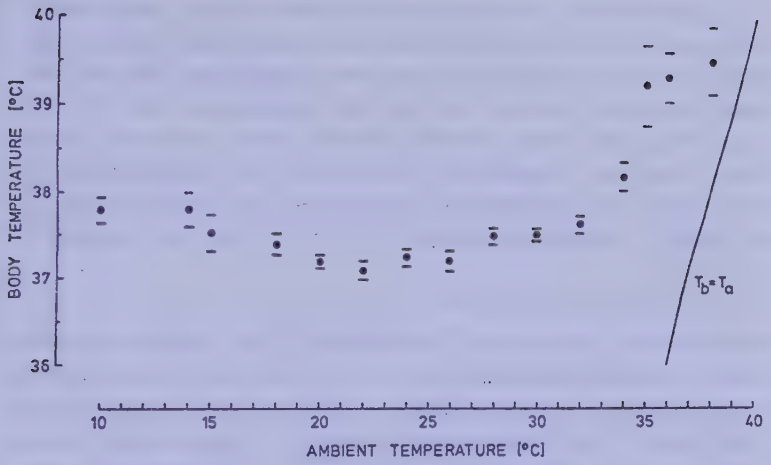


Fig. 2 Body temperature at varying ambient temperatures measured in 6 fennecs after exposures of 4 to 6 hours to $T_a$s below 34 °C and of 2.5 to 5.5 hours to $T_a$s between 34 °C and 38 °C. The circles represent means, horizontal lines denote SE.

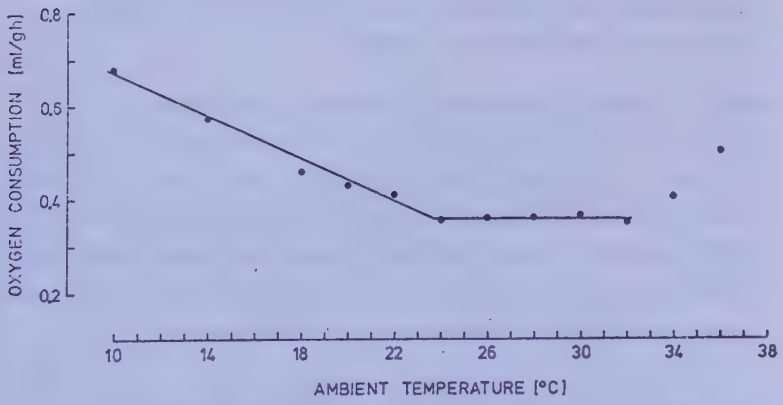


Fig. 3 Oxygen consumption of 5 fennecs as a function of ambient temperature (M = 1,106 g). The line below 24 °C fitted to the data by the method of least squares has the equation: RMR = 0.897 - 0.023 $T_a$. Below 36 °C each circle represents the mean from 11 to 17 measurements (0.01 ml/gh $\leq$ SE $\leq$ 0.03 ml/gh). The mean at 36 °C is based on 8 runs (SE = 0.05 ml/gh).

The slope of this line indicates a minimal thermal conductance C of 0.023 ml/g h °C. The lower critical temperature ($T_{lc}$) determined by the intersection of the RMR/$T_a$-regression line and the basal metabolic rate is 23.4 °C. When extrapolated this line intersects the abcissa at a $T_a$ of 39 °C which is slightly above the average body temperature of the fennec. At thermoneutrality the respiratory quotient (RQ) amounts to 0.84; while panting at ambient temperatures above 34 °C, the RQ sometimes exceeds 1.

## 1.4 Evaporative Water Loss

The effect of environmental temperature on the evaporative water loss in fennecs expressed both as a function of body mass and of oxygen uptake is shown in Figs. 4 and 5. The mass relative water loss (Fig. 4) is rather constant at ambient temperatures between 10 °C and 30 °C ranging from 0.65 mg/g h to 0.91 mg/g h. It increases sharply when $T_a$ exceeds 32 °C reaching the 3.5 fold of the average water loss in the thermoneutral zone at a $T_a$ of 38 °C. The ratio of water evaporated to oxygen consumed (Fig. 5) below a $T_a$ of 32 °C can be described by a regression line with the equation: log EWL (mg $H_2O$/ml $O_2$) = 0.020 $T_a$ (°C) - 0.255 (correlation coefficient r = 0.983).

Table 2 Level of evaporative cooling in the fennec

| $T_a$ (°C) | 10 | 14 | 18 | 24 | 28 | 32 | 36 | 38 |
|---|---|---|---|---|---|---|---|---|
| $\frac{EHL}{HP} \cdot 100$ (%) | 11.3 | 13.1 | 18.2 | 24.0 | 30.1 | 35.5 | 51.6 | 55.7 |

EHL = Heat lost by evaporation, HP = Heat produced

Assuming that the evaporation of 1 mg $H_2O$ dissipates 2.43 J (= 0.58 calories) and that 1 ml $O_2$ releases 20.34 J (= 4.86 calories; mean RQ = 0.85), the rate of heat lost by evaporation (EHL) can be expressed as percentage of the heat produced (HP). The level of evaporative cooling is directly related to ambient temperatures between 10 °C and 38 °C:

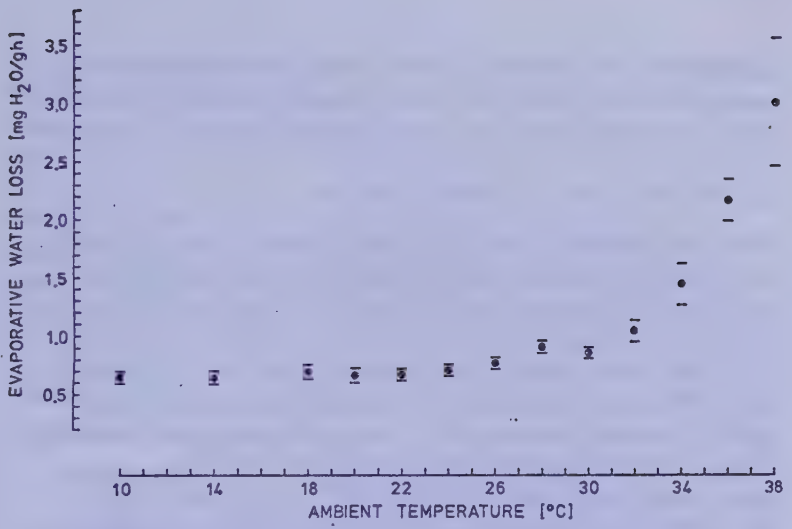


Fig. 4 The relationship between evaporative water loss expressed as a function of body mass and ambient temperature. Circles denote the means from 3 fennecs, horizontal lines represent SE (10 to 16 measurements at each $T_a \leqq 36$ °C, 5 measurements at a $T_a$ of 38 °C).

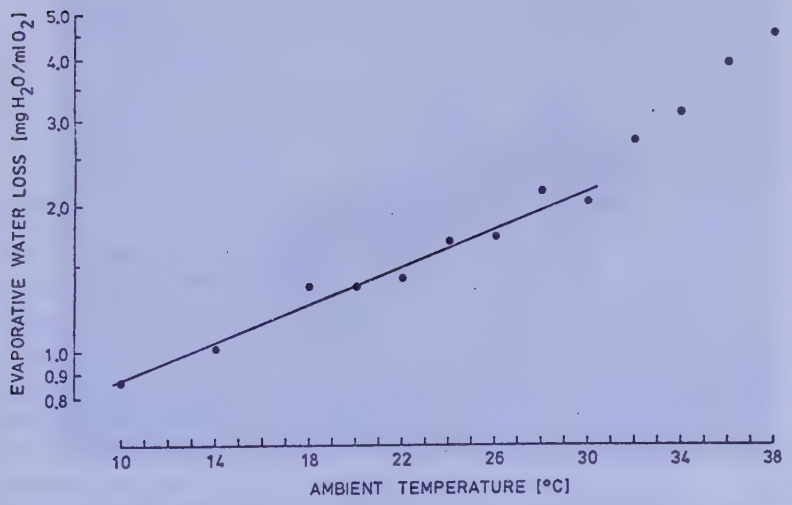


Fig. 5 Ratio of evaporative water loss to oxygen consumption at varying ambient temperatures. The line fitted to the data below 32 °C has the equation
$\log EWL\ (mg\ H_2O/ml\ O_2) = 0.020\ T_a\ (°C) - 0.255$ .

$\log\left(\frac{EHL}{HP} \cdot 100\ (\%)\right) = 0.025\ T_a\ (^{\circ}C) + 0.786$; correlation coefficient $r = 0.990$. At a $T_a$ of 38 °C, however, at most 75 % (mean 56 %) of the metabolic heat can be lost by evaporation (Table 2).

## 1.5 Heat Production in Newborn Fennecs

In captivity natural rearing of young fennecs as well as artificial breeding is rather difficult and very seldom (Koenig, 1970; Kühme, 1973; Melchior, 1976). In the years 1976 and 1977, a young couple of fennecs (♀ born in 1973, ♂ born in 1975) had two litters. After a gestation of 50 days, two young were born on may 20th, 1976. They were eaten three days later. On august 8th, 1977, the female whelped three strong fennecs after a gestation of 51 days. As at that time, the surroundings were rather noisy, the young were removed from their mother several hours after birth to prevent her from eating them. The young were fed special milk (Ipevet-milk, Leatherland Ltd./Surrey-England).
From the first day of life, $T_b$ and oxygen uptake were measured using a small plexiglass cylinder (2.4 l; flow rate 25 l/h). The young were surprisingly vivid but nevertheless died after the first week of life without any obvious cause. Possibly they got milk in the lungs for they often swallowed the wrong way. This was also observed by Koenig (1970) and Melchior (1976).

Fig. 6 Fennec at the age of two days. Paws and ears are not yet furred.

Table 3 shows the metabolic response of 3 one-day-old fennecs to ambient temperatures of 16 °C and 28 °C, respectively. Body temperature of the young is markedly below the adult level averaging only 31.8 °C at a nest-temperature of 27 °C. From the first day of life fennecs are able to sense changes in ambient temperature. Heat production at a $T_a$ of 16 °C is about 31.4 % higher (range 17 % - 43 %) compared to the rate at 28 °C. Body temperature, however, cannot be maintained yet. In cold, the young are restless crawling all round the respirometer chamber.

Table 3 Metabolic response of 3 fennecs on their first day of life when exposed to a $T_a$ of 16 °C and to a $T_a$ of 28 °C, respectively, for 30 minutes.

| $T_a$ (°C) | MR (ml/gh) | RQ | $T_{b1}$ (°C) | $T_{b2}$ (°C) | $\Delta T_b$ (°) | M (g) |
|---|---|---|---|---|---|---|
| 16 | 0.699 | 1.061 | 31.6 | 23.5 | -8.1 | 44.3 |
| 28 | 0.532 | 0.881 | 32.0 | 29.2 | -2.8 | 44.1 |

MR = Metabolic rate; M = Body mass
$T_{b1}$= Body temperature at the beginning of the test
$T_{b2}$= Body temperature at the end of the test

CARDIOVASCULAR ADAPTATIONS

2.1 Diurnal Heart Rate

Diurnal variations of heart rate are shown in Fig. 1. In four completely undisturbed animals (M = 1,156 g) heart rate was measured continuously by telemetry for altogether 80 days. The circadian course of HR largely corresponds with that of body temperature. Average heart rate during daytime amounts to 118 $min^{-1}$ showing a minimum of 109 $min^{-1}$ at 16.00. With beginning darkness, HR rises within one hour up to 137 $min^{-1}$. In the animals' activity period, heart rate increases gradually to the

maximum mean of 154 $min^{-1}$. After this peak which occurs at 5.00, HR decreases markedly to 120 $min^{-1}$ at 10.00. Overall heart rate runs up to 130 $min^{-1}$.

## 2.2 Heart Rate at Various Ambient Temperatures

Heart rate was determined in four fennecs exposed to a given $T_a$ for 4 to 6 hours. No recordings were taken during the initial 2.5 hours. Resting heart rate (RHR) is inversely related to ambient temperatures between 10 °C and 24 °C (Fig. 7) as described by the least-squares regression line with the equation RHR ($min^{-1}$) = 139.86 - 2.73 $T_a$ (°C); correlation coefficient r = 0.990. Basal heart rate in the thermoneutral zone amounts to 74.6 ± 1 $min^{-1}$ (40 measurements; M = 962 g). The regression line of RHR on $T_a$ strikes this value at a $T_a$ of 23.9 °C which is slightly above the lower critical temperature ($T_{lc}$) resulting from oxygen uptake measurements.

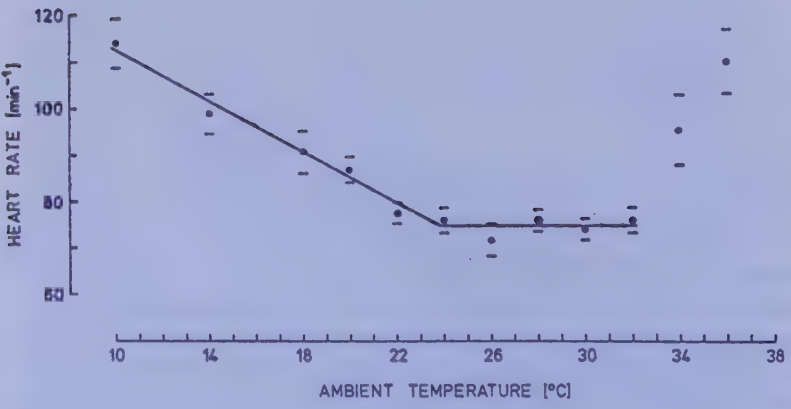


Fig. 7 Resting heart rate of 4 fennecs as a function of environmental temperature (M = 962 g). The least-squares regression line below thermoneutrality has the equation: RHR ($min^{-1}$) = 139.86 - 2.73 $T_a$ (°C).

## 2.3 Heart Rhythm

Typical of all fennecs used in this study is an irregular heart rate varying in time with the respiration. This arrhythmia is well marked in thermoneutral environment and in sleeping animals, however, it is hardly noticed during activity, and it lacks completely in panting fennecs (Fig. 8). The extent of the arrhythmia (variance of heart beat intervals; Koepchen & Thurau, 1959) increases from 10 °C to 30 °C (Variance (msec) = 2.67 $T_a$ (°C) - 5.43; correlation coefficient r = 0.835).

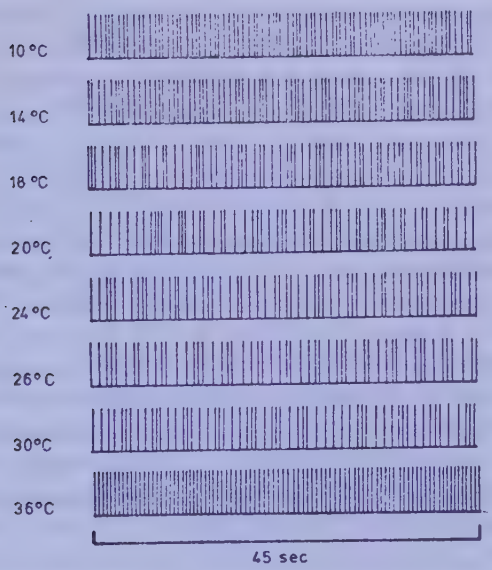


Fig. 8 Examples of heart rate patterns in the fennec graphed according to ECG recordings at various ambient temperatures. The animal was asleep at all temperatures except at a $T_a$ of 36 °C where panting occurred.

## DISCUSSION

### Body Temperature

The mean body temperature of the fennec does not differ essentially from that of other mammals. In the daily course of $T_b$, the peak at 6.00 might be due to an increased activity at 'dawn'. Koenig (1970) reports the main activity of fennecs to occur between 2.00 and dawn (presumably natural photoperiod), whereas the animals usually sleep from dawn to beginning darkness with only short interruptions. According to Kavanau & Ramos (1975) the kitfox (Vulpes macrotis) which is nocturnal in the main, has a predominating dawn activity, too.
Fennecs have only little tolerance to high ambient temperatures (Table 1). Above a $T_a$ of 32 °C their $T_b$ rises quickly to a critical value. Panting starts at a relatively moderate body temperature. This agrees with the observations of Hemingway (1938) and Robinson & Lee (1941) in dogs. According to Gauthier-Pilters (1962, 1967) fennecs avoid sunshine in captivity as soon as the temperature on the ground exceeds 36 °C. In the Algerian Sahara, 50 days old fennecs, kept above the ground, successfully sustained a $T_a$ of 44 °C in the shade for several hours panting loudly and drinking water avidly (Koenig, 1970). Usually, however, fennecs do not often have to face such extremely high ambient temperatures because, except in winter, they spend the daytime in burrows (Gauthier-Pilters, 1967) at moderate or cool ambient temperatures which never exceed 34 °C (Kirmiz, 1962; Shalaby, 1966; Carpenter, 1966). Petter (1961) states that even in the warmest months in summer, nocturnal temperatures in Beni-Abbès, Algerian Sahara, are in the range of 25 °C - 30 °C. When used to live outdoors, fennecs resist cold very well and endure even $T_a$s of -25 °C and -28 °C (Hutzelsider, 1941; Philippović, 1941; Gauthier-Pilters, 1967).

### Oxygen Consumption, Conductance and Thermoneutral Zone

The basal metabolic rate of fennecs is considerably reduced (Table 4) amounting to only 60.7 % of the level predicted on

the basis of body mass ($3.4\ M\ (g)^{-0.25}$; McNab, 1966). As in many desert rodents this may be regarded as an adaptation to the desert environment because it minimizes the endogenous heat load (McNab & Morrison, 1963; McNab, 1966; MacMillen & Lee, 1970).

Table 4 Basal metabolic rate and body temperature of some carnivores.

| | M (g) | BMR (ml/gh) | BMR % | $T_{lc}$ (°C) | $T_b$ (°C) | References |
|---|---|---|---|---|---|---|
| Dog | 9,666 | 0.342 | 99.7 | 24 | 38.0 | Hammel et al., 1958 |
| White fox[1)] | 4,700 | 0.526 | 128.1 | $\leq -30$ | 37.9 | Scholander et al., 1950; Irving & Krog, 1954 |
| Red fox | 4,440 | 0.550 | 132.0 | 8 | 38.7 | Irving & Krog, 1954 Irving et al., 1955 |
| Fennec | 1,106 | 0.358 | 60.7 | 24 | 38.1 | Present study |

BMR % = 100 BMR / $3.4\ M^{-0.25}$ (McNab, 1966)

1) average values of 3 white foxes calculated according to data from Scholander et al., 1950, assuming a conversion factor of 4.8 calories/ml $O_2$.

Fennecs have a wide thermoneutral zone which, during summer, includes the range of ambient temperatures in the burrow and usually nocturnal air temperatures, too (see above). Together with the low basal metabolic rate, this certainly is an advantage by reducing the energy requirements of the fennec.
The minimal conductance is only 77 % of the value expected by body mass according to the formula of Herreid & Kessel (1967). This suggests that fennecs are well adapted, too, to low ambient temperatures. Similar results were obtained by Carpenter (1966) in kangaroo rats. McNab (1970) states that species living in deserts have a low BMR and therefore must have a reduced conductance to maintain their body temperature.

## Heat Production in Newborn Fennecs

Body temperature of neonate fennecs is about 6.3 ° below that of adults. This was also observed in the dog (Jensen & Ederstrom, 1955). Generally it is presumed that the low $T_b$ is due to a lowering of the set point in the thermoregulatory system. The metabolic response to cold shows that fennecs are able to sense ambient temperatures from the first day of life. This is in accordance with Koenig (1970) who studied growth and behaviour of fennecs. As in newborn dogs (McIntyre & Ederstrom, 1958), the increase in heat production on cold exposure is not sufficient during the first days of life to maintain the body temperature at a constant level.

## Evaporative Water Loss

In the temperature range between 18 °C and 29 °C, average evaporative water loss is related to body mass by the equation $EWL\ (g/h) = 2.58\ M\ (kg)^{0.826}$ (Chew, 1965). Many desert rodents have reduced rates of pulmocutaneous water loss e.g. Dipodomys spectabilis 20.7 %, D. merriami 26 %, Perognathus spp. 32 % (Schmidt-Nielsen & Schmidt-Nielsen, 1950). The fennec, too, has a low rate, evaporating only about 30 % of the predicted value at a $T_a$ of 24 °C, contrary to the carnivorous grasshopper mouse which loses 98 % as much as is expected on the basis of body mass (Whitford & Conley, 1971). The authors conclude that a reduction in pulmocutaneous water loss is unnecessary for a carnivorous animal, the prey of which contains sufficient water. Yet the fennec shows a significant reduction; possibly this may be a reflexion of the low metabolic rate which, too, lacks in the grasshopper mouse. The low EWL in the fennec is an advantage at moderate and cool ambient temperatures as it is the case in the burrows and usually at night. When exposed to high $T_a$s, however, this is unfavourable. As the fennec loses only about 56 % of the metabolic heat at a $T_a$ of 38 °C, its body temperature must soon increase.

Heart Rate

The daily courses of heart rate and $T_b$ closely coincide, although only HR was measured telemetrically. The relatively large difference between the heart rates of resting animals as obtained in the respirometer chamber (74.6 $min^{-1}$; M = 962 g) and free-ranging in a room (118 $min^{-1}$; M = 1,156 g), respectively, may be explained by the following facts: the animals were used to sleep deeply shortly after being placed in the respirometer chamber. Probably they are much more alert while resting together with some other fennecs, thus not showing a true 'basal' heart rate. Besides this, heart rates taken in the metabolic chamber are means from recordings of 60 minutes duration, whereas in the daily cycle of HR the data of 12 hours were averaged. Consequently, the time to fall asleep and to wake up as well as short activity periods are included. Basal heart rate is considerably reduced. It amounts to only 51 % of the value according to the formula of Hudson (personal communication to Leitner, 1966; Wang & Hudson, 1971) which is based on measurements within the thermoneutral zone: HR ($min^{-1}$) = 816 M $(g)^{-0.25}$. The reduced BHR of fennecs may allow a wider range to rise HR under unfavourable conditions. This was discussed also for chipmunks (Jones & Wang, 1976).

The amount of oxygen transported per heart beat (oxygen pulse, OP) can be calculated over the range of ambient temperatures for which oxygen consumption and heart rate are known. Table 5 shows that the $O_2$-pulse rises with decreasing $T_a$. The contribution of heart rate to the increased oxygen requirements below the lower critical temperature ($T_{lc}$ = 23.4 °C), too, increases steadily as $T_a$ drops (Table 5). This suggests that at low ambient temperatures the increased $O_2$ demands are met essentially by an increase in heart rate rather than by changes in stroke volume and arteriovenous differences in $O_2$ content, respectively. This agrees with the observations in the mastiff bat (Leitner, 1966), in chipmunks (Wunder, 1970; Jones & Wang, 1976) and in flying foxes (Noll, personal communications).

Table 5 Variations of the oxygen pulse and contribution of heart rate to the increased oxygen demands below thermal neutrality in fennecs.

| $T_a$ (°C) | RHR ($min^{-1}$) | OP µl/beat | Contribution of HR | |
|---|---|---|---|---|
| | | | %a | %b |
| 10 | 114.2 | 98.2 | 65.3 | 72.1 |
| 14 | 99.0 | 92.7 | 61.0 | 67.8 |
| 18 | 90.7 | 88.8 | 57.5 | 66.1 |
| 22 | 77.4 | 81.6 | 36.1 | 36.1 |
| TNZ | 74.6 | 76.6 | - | - |

a The values given are increases relative to the TNZ
b The values represent the increase to the next highest $T_a$

$$\text{Contribution of HR (\%)} = \left[\frac{HR - hr}{hr}\right] : \left[\frac{HR - hr}{hr} + \frac{OP - op}{op}\right]$$

(Bartholomew & Tucker, 1963)
hr, op indicate the initial state;
HR, OP indicate the changed state.
Theoretical OP in the TNZ: 66.8 µl/beat (M = 962 g), combined equation (McNab, 1966; Wang & Hudson, 1971)

Koepchen & Thurau (1965) studied the respiratory arrhythmia in dogs and found that there is a close correlation between the extent of the arrhythmia and the influence of the vagus nerve which essentially affects heart rate. If the heart rate of fennecs is varied by changing the environmental temperature between 10 °C and 32 °C, there is such a relation, too, (Fig. 9) which can be described by the equation
$\log var_{HI}$ (msec) = 2.5 log HI (msec) - 5.55 ; (correlation coefficient r = 0.946). $Var_{HI}$ denotes the variance of the heart-beat intervals in place of the arrhythmia, and the mean heart-beat interval HI is a measure for the influence of the vagus nerve on the heart (refer to Koepchen & Thurau, 1959).

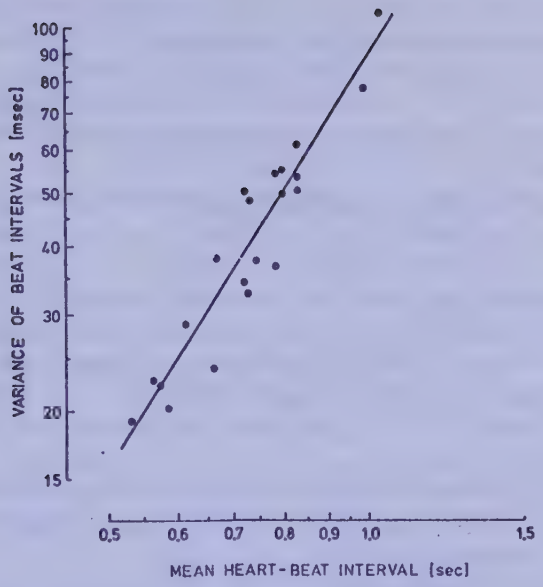


Fig. 9 Relation between the arrhythmia of the heart (variance of beat intervals) and the influence of the vagus nerve (mean heart-beat interval) in 3 fennecs. Each point is based on a 30 sec period which corresponds to 9 - 11 respiration cycles. Variation of heart rate was obtained by changing the environmental temperature from 10 °C to 32 °C.

Fennecs show many physiological adaptations for desert life, although they usually avoid intense heat by behavioural adjustments (burrowing, nocturnal activity). They have not only a considerably reduced basal metabolic rate and a low minimal conductance, a depressed evaporative water loss and great cardiovascular reserves, but, in addition, they are able to subsist on the body water of their prey and to produce a remarkably concentrated urine (part II).

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THERMOREGULATION, HEART RATE AND WATER BALANCE IN THE FENNEC

FENNECUS ZERDA (ZIMM.)

Part II: WATER BALANCE AND KIDNEY STRUCTURE IN THE FENNEC

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## ABSTRACT

1. Water balance and urine concentrations were determined in fennecs under regimens of different water and protein content.

2. In the absence of heat stress fennecs are able to subsist on a diet of whole mice for at least 100 days. Probably they can survive without drinking water for an indefinite time. Mean gain of body mass was 7.9 % of the initial value (maximum 33 %).

3. Total water intake is 5.6 % of body mass which equals only 55 % of the predicted rate.

4. Evaporative water loss is considerably reduced. The basal rate amounts to only 0.77 mg/g h; including the hours of activity, fennecs evaporate 1.11 mg/g h at an ambient temperature of 26 °C. These are 31 % and 45 %, respectively, of the expected value.

5. Fennecs have a powerful kidney. When fed on mice only, urine concentrations are in the range from 1480 to 3828 mOsm/l with a mean of 2618 mOsm/l. Urea concentration averages 1991 mM/l. The maximum urine concentration of 4022 mOsm/l was observed in an animal on restricted water intake.

6. In contrast to the red fox whose renal medulla forms a crest, the fennec has a distinct papilla (relative medullary thickness = 5.4). Kidney structure and concentrating ability are correlated as in many other mammals.

## INTRODUCTION

Burrowing and nocturnal habits, a low rate of evaporation and a high concentrating ability of the kidney are important factors in water conservation generally related to rodents in an arid environment. Studies on the desert mulgara (Schmidt-Nielsen & Newsome, 1962) and the grasshopper mouse (Schmidt-Nielsen & Haines, 1964) suggest that in the absence of heat stress, wild carnivorous mammals should remain in water balance on a diet of fresh meat. The fennec is the only carnivore of the Sahara desert found far away from oasis and water (Dekeyser & Derivot, 1959), but there are no details available on the water balance of this small fox. One objective of this study, therefore, was to examine the fennecs' ability to sustain water balance on a diet of laboratory mice without drinking water. In addition, the correlation between kidney structure and kidney function was studied as well as the water turnover under conditions of reduced water intake.

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## MATERIALS AND METHODS

### Animals and Maintenance

The fennecs used in this study were captured in Southern Tunisia in the years 1974 and 1976. They were kept at an ambient temperature of 25 ± 1 °C and a relative humidity of 50 ± 5 % under a timed light cycle of 12 L : 12 D. The animals usually did not urinate during the resting period (lights on from 20.30 to 8.30) which allowed an optimal collection of urine and faeces throughout the activity period. The animals could adjust to these conditions and to the necessary handling for about two weeks prior to measurements.
During the experiments the fennecs were housed individually in wooden boxes (50 x 45 x 45 $cm^3$) with a wire-mesh floor and with a sliding front-door which allowed to feed the animals and to catch them easily to determine their body mass (M). The boxes were placed above a drawer of water-repellent coating (Resicoat, Bosch-Gruppe, Reutlingen, W.-Germany).

### Experimental Regimens

The fennecs were given a pre-weighed amount of food five times a day during the first eight hours of the activity period. After 20 minutes, the remaining food was withdrawn from the animal to minimize the error due to evaporation. When water was available (regimen III), the fennecs were allowed to drink a certain amount of water twice a day. They had no supplementary vitamines during the experimental period.
The water content of food-samples was determined by oven-drying them to constant mass. The percent of fat, carbohydrate and protein of the food was calculated according to Bailey et al. (1960) in mice and from the Geigy-Tabellen (7th edition) for bananas. The quantity of protein digested was determined from the amount of urea lost per day. Based on this value and assuming a complete digestion of carbohydrate and fat, metabolic water production from the food consumed was calculated by means of the metabolic water values in the Geigy-Tabellen.

### Collection and Analysis

Every morning the animals were weighed to the nearest 0.5 g. To determine fecal water loss, faeces were weighed directly when voided and then oven-dried at 104 °C to constant mass. Urine samples were collected by pipette immediately when voided. The pH of urine samples was determined by use of indicator-paper (Macherey-Nagel + Co, Düren, W.-Germany), osmolality was measured with an osmometer (Knauer, Berlin, W.-Germany) by the freezing point depression method. Concentrations of urea were determined on the basis of the Berthelot reaction (Merck, Merckotest 3334, Darmstadt, W.-Germany) by means of a photometer (Eppendorf 1101 M, Hamburg, W.-Germany) at 578 nm.

# RESULTS

## WATER TURNOVER AND URINE CONCENTRATION

### 1 Food Intake and Composition of Food

Total food intake at various diets and the composition of the food consumed is summarized in Table 1.
Diet I and III are low-protein regimens with considerable amounts of carbohydrate. Related to diet I, the water content of diet III is reduced for about 33 %. During this series the animals were offered some additional drinking water in order to make sure the consumption of approximately the same amount of dry food as in diet I. Thus, a decrease in body mass could be regarded as the effect of dehydration and was not due to a reduced food intake.

Table 1 Water content and composition of various regimens and total food intake

| | Diet | Body mass (g) | Water content (%) | Drinking water ml/day | Total food intake g/day | Total food intake g/kg day | Dry food intake g/day | Dry food intake g/kg day |
|---|---|---|---|---|---|---|---|---|
| I | Bananas Mice | 1290 | 74.6 | - | 93.3 | 72.3 | 23.7 | 18.4 |
| II | Mice | 1277 | 68.0 | - | 85.2 | 66.7 | 27.3 | 21.4 |
| III | Hap[1] Mice Bananas | 1168 | 50.3 | 23.1 | 43.2 | 37.0 | 21.5 | 18.4 |

1) commercial dry dog-chow (Effem, W.-Germany)

| Diet | Fat g/day | Fat g/kg day | Carbohydrate g/day | Carbohydrate g/kg day | Protein consumed g/day | Protein consumed g/kg day | Protein digested g/day | Protein digested g/kg day |
|---|---|---|---|---|---|---|---|---|
| I | 3.4 | 2.6 | 11.6 | 9.0 | 7.3 | 5.7 | 6.0 | 4.7 |
| II | 7.8 | 6.1 | - | - | 16.0 | 12.5 | 13.3 | 10.4 |
| III | 3.2 | 2.7 | 9.3 | 8.0 | 6.8 | 5.8 | 6.4 | 5.5 |

Although this regimen dehydrated the animals only slightly, they waited avidly for their daily water rations.
Diet II, which consists solely of freshly killed laboratory mice, resembles mainly the fennecs' food habits in the wild. It represents a protein-rich food of high water content.

Table 2 Water turnover in the fennec at various diets

| Diet | Body mass (g) | ΔM/day (g) | Total water intake | | Total water output | |
|---|---|---|---|---|---|---|
| | | | g/day | g/kg day | g/day | g/kg day |
| I | 1290 | -1.1 | 82.1 | 63.6 | 82.1 | 63.6 |
| II | 1277 | +0.7 | 71.6 | 56.1 | 71.6 | 56.1 |
| III | 1168 | -3.1 | 56.0 | 47.9 | 57.7 | 49.4 |

| Diet | Fecal water loss | | Urinary water loss | | Insensible water loss | |
|---|---|---|---|---|---|---|
| | g/day | g/kg day | g/day | g/kg day | g/day | g/kg day |
| I | 10.9 | 8.5 | 39.7 | 30.8 | 31.5[1] | 24.4 |
| II | 5.7 | 4.5 | 31.9 | 25.0 | 34.0[1] | 26.6 |
| III | 11.1 | 9.5 | 15.8 | 13.5 | 30.8[2] | 26.4 |

1) Since body mass was relatively constant during the days on which faeces and urine were collected, insensible water loss IW (= water lost by evaporation) was calculated according to the equation: IW = total water intake - water in urine - water in faeces (Chew, 1965)

2) Insensible water loss was estimated on the basis of insensible mass loss (IL): IW = IL x (IW/IL), (Chew, 1965). The quotient IW/IL was determined in measurements of metabolic rate and evaporative water loss at a $T_a$ of 26 °C (see part I)

The values for insensible water loss reported in Table 2 include hours of activity. The rates are somewhat higher than the basal rates found in simultaneous measurements of basal metabolic rate and evapoartive water loss (part I).

## 2 Water Balance in the Fennec

Daily water intake and water turnover of fennecs are detailed in Table 2. Total water intake (free water in food + metabolic water + drinking water, if available) decreases from 6.4 % of body mass on diet I to 5.6 % on the diet of mice and to only 4.8 % on regimen III. Urine output is directly related to water intake, the actual volume of urine on diet III reaches only 40 % and 50 %, respectively, of the amount produced on diet I and II. The evaporative water loss, however, differs only slightly on the different experimental regimens. Thus, most water conservation during water restriction is effected by a reduction in urinary water loss. Evaporation, therefore, is the limiting factor in the fennec's water balance.
The changes in body mass cited in Table 2 are derived from those days on which urine and faeces were collected. Related to the whole period of a given diet, the animals gain 1.3 % of the initial body mass after 35 days on diet I, but they lose 7.5 % within 30 days on diet III. (Diet II: see 4)

## 3 Urine Concentration and Water Content of the Faeces

Urine concentration reflects very well the conditions of the different regimens (Table 3, Table 2). A reduction in water intake of 32 % (diet I, III) leads to a similar increase in both urine osmolality and urea concentration as a reduction of only 12 % combined with the double protein load (Diet I, II).
When the animals were fed mice, urine osmotic concentration fluctuated between 1480 and 3828 mOsm/l. On a mixed diet of mice

Table 3 Urine osmolality, pH and urea concentration in fennecs submitted to different regimens

| Diet | pH | Urine (mOsm/l) | Urea (mM/l) | Number of samples | Animals |
|---|---|---|---|---|---|
| I | 7.1 | 1129 ± 32 | 738 ± 27 | 80 | 4 |
| II | 6.5 | 2618 ± 29 | 1991 ± 35 | 150 | 6 |
| III | 6.9 | 2548 ± 89 | 1549 ± 68 | 50 | 3 |

and bananas, it was in the range of 581 to 2167 mOsm/l. The maximum urine osmolality of 4022 mOsm/l was found in a male submitted to diet III. The highest urea concentration measured was 3095 mM/l.
The amount of dry faeces is fairly constant (4.2 g/kg day on diet I and II, 4.1 g/kg day on diet III). Fecal water loss is smallest on regimen II (51 %).

## 4 Changes in Body Mass during a Long-Termed Diet of Mice

Within a group of four fennecs fed on laboratory mice but deprived of drinking water, the changes in body mass were controlled for 100 days (Fig. 1). After an initial loss, body mass increases showing marked differences between the individual animals. At the end of the series, mean gain amounts to 7.9 % of the initial body mass. The maximum increase of 33 % occurred in a two years old female. Urine osmotic concentration did not increase with preceeding experimental time. After 100 days, three of the four fennecs were not at all interested in drinking water. However, the old male (lowest graph in Fig. 1), which had lost some body mass, drank 90 ml within a few minutes.
The data indicate that at moderate ambient temperatures fennecs are able to sustain their water balance for an indefinite time from the body water of their prey.

## 5 Effect of Severe Water Deprivation

Two animals were subjected to a diet containing only 32 % of free water (Hap, dry bananas) but 12 % of protein. As soon as drinking water was withdrawn, both animals reduced their food intake. On the 2nd day (male) and on the 3rd day (female), respectively, they refused completely to eat anything. Their activity decreased markedly. After three days without water they had lost 8.6 % of the initial body mass. Urinary water loss was considerably reduced, evaporative water loss (estimated from IL) was somewhat affected, too. When water was offered again on the fourth day, the male drank 66 ml = 4.9 % of body mass at a time; the female consumed 49 ml = 4.0 % by and by. The animals immediately began to eat as before. Urine osmotic concentrations did not exceed the maximum value reported in diet III.

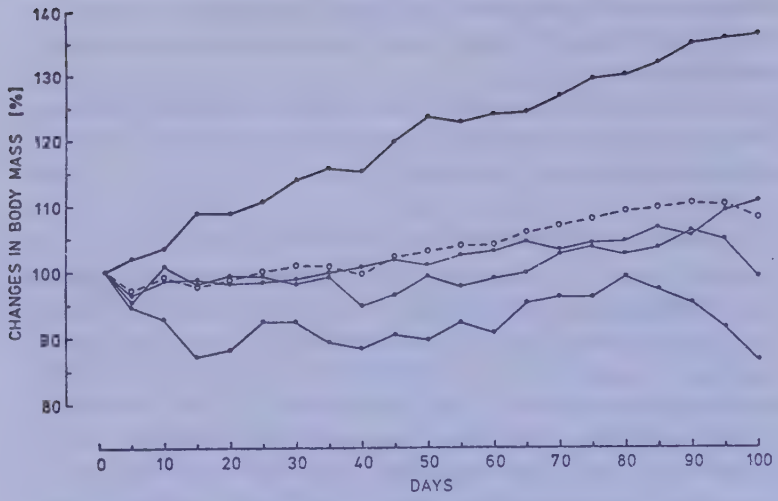


Fig. 1 Changes in body mass in 4 fennecs fed laboratory mice only. Closed symbols represent the individual animals, open symbols denote mean values.

KIDNEY STRUCTURE OF FENNEC AND RED FOX

Because of the relatively high concentrating ability of the fennecs' kidney, its structure was examined. Therefore, immediately after death, the kidneys of four fennecs were dissected out, preserved in Stieve, Orth, Susa and Bouin fluid, respectively, and cut at 8 microns. In addition, the kidneys of several specimens of red foxes (Vulpes vulpes) preserved in formalin were examined, too.

The fennec has a simple kidney of the primitive type (Sperber, 1944). The medulla is devided into outer and inner zone and forms a distinct papilla (Fig. 2). In contrast, the kidney of the red fox shows a crest (Fig. 3).

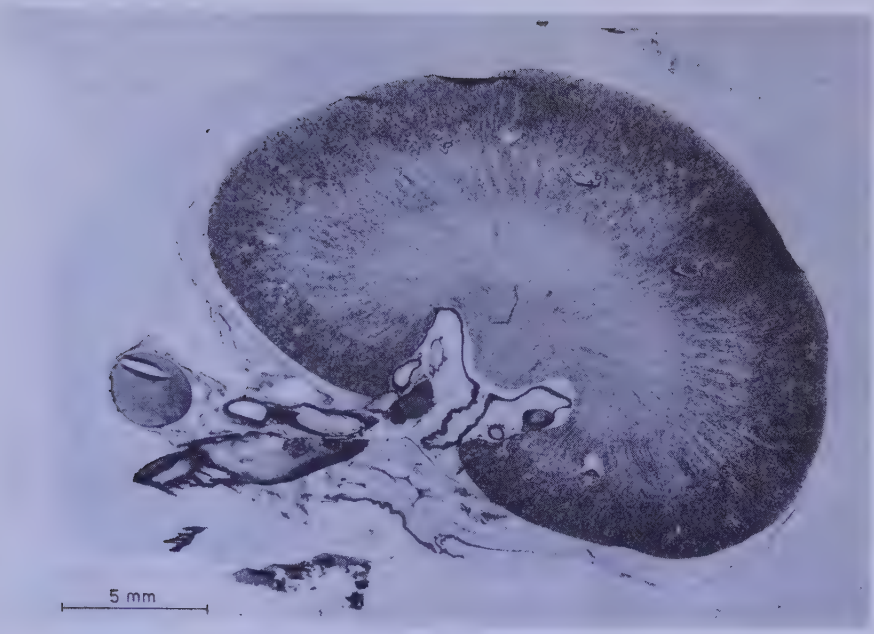


Fig. 2 Sagittal section of the fennec's kidney. (Azan stain; shrinkage 11.9 %)

Table 4 Kidney type, kidney size and relative medullary thickness (RMT) of fennecs and red foxes

| | Kidney type | Kidney size | | Actual medulla (mm) | RMT |
|---|---|---|---|---|---|
| | | mean (mm) | range (mm) | | |
| Fennec [1] | papilla | 18.4 | 14.8 - 20.8 | 9.8 | 5.4 |
| Red fox [2] | crest | 32.9 | 29.7 - 35.0 | 13.5 | 4.1 |

1) four animals; values are derived from fresh kidneys
2) six animals; values are derived from formalin-preserved kidneys

Kidney size equals the cube root of the product of the kidney's dimensions. Relative medullary thickness is defined as follows: 10 times the thickness of the medulla devided by the kidney size (Sperber, 1944).

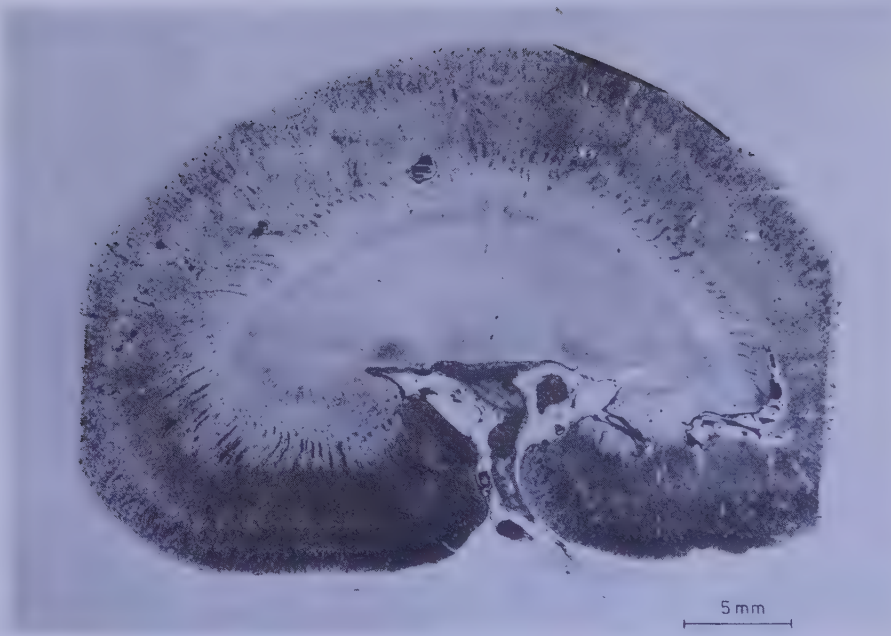


Fig. 3 Sagittal section of the red fox kidney.

## DISCUSSION

Like the mulgara (Schmidt-Nielsen & Newsome, 1962), the grasshopper mouse (Schmidt-Nielsen & Haines, 1964) and like cats (Prentiss et al., 1959), fennecs are able to maintain or gain body mass on a diet of whole mice and fresh meat, respectively, without supplementary drinking water. Under these conditions the mean daily ad. lib. water intake in the fennec is only 55 % as much as is predicted on the basis of body mass according to the equation: $I\ (g/h) = 0.01\ M(g)^{0.88}$ (Adolph, 1949). Taking into account that the fennec may supplement its food by succulent plants of high water content (70 % – 94 %; Bailey, 1923) and by insects (60 % - 85 % $H_2O$; Schmidt-Nielsen et al., 1952), the daily water needs are largely guaranteed. In contrast to the grasshopper mouse (Whitford & Conley, 1971), fennecs conserve much water by a low evaporative water loss. Basal EWL

amounts to only 31 % of the expected rate (part I), evaporative water loss all day long is lowered to 45 % (Table 2; IW (ml/h) = = 2.58 $M(kg)^{0.826}$, Chew, 1965). Whereas fecal water loss is within the range reported for nocturnal rodents (MacMillen, 1972), daily urine production is considerably reduced amounting to only 59 % of the expected level (U (ml/h) = 0.0064 $M(g)^{0.82}$; Adolph, 1949). During dehydration (diet III), there is little or no change in evaporative water loss but a pronounced reduction in urine volume. The reduced urinary output in diet III as compared to diet II represents a daily water conservation of 14.6 ml, which in view of the water balance would enable the fennec to compensate the increased evaporative water loss at a $T_a$ of 36 °C for 5.25 hours (EWL = 2.18 mg/gh = 2.78 g/h; M = 1277 g) and at a $T_a$ of 34 °C for nearly 8 hours (EWL = 1.45 mg/gh = 1.85 g/h); see part I). However, the fennec does not tolerate temperatures above 32 °C for such a long time: dissipating only 56 % (maximum 75 %) of the metabolic heat by evaporation, body temperature soon increases (part I).

The ability to conserve physiologically useful water by minimizing urinary water loss depends on an efficient kidney. Although not attaining the extreme osmotic concentrations found in xeric-adapted rodents which are independent of exogenous water (4090 mOsm/l in Dipodomys spec., 5540 mOsm/l in D. merriami; Schmidt-Nielsen, 1964; Abbott, 1971), fennecs are able to concentrate urine to higher values than other carnivores (Table 5). Maximum urine concentration and renal medullary thickness are according the relationship reported by Schmidt-Nielsen & O'Dell, 1961 (Table 5).

Table 5 Relative medullary thickness (RMT) and maximum urine concentration in some carnivores

| | Kidney type | RMT | Urine conc. mOsm/l | References |
|---|---|---|---|---|
| Dog | crest | 4.3 | 2608 | Sperber, 1944 |
| Cat | papilla | 4.8 | 3118 | Schmidt-Nielsen & O'Dell, 1961 |
| Fennec | papilla | 5.4 | 4022 | Present study |

## Conclusions

The above considerations suggest that the major difficulty in the fennec's desert life is not the scarcity of water in the habitat but rather its intolerance to cope with high ambient temperatures. Although fennecs have many metabolic and cardiovascular adaptations (reduced basal metabolic rate, wide thermoneutral zone, low minimal conductance, reduced heart rate; part I) as well as powerful water conserving mechanisms by a reduced evaporative water loss and a considerable concentrating ability of the kidney, they are, after all, well adapted to their environment only because they avoid extremely high ambient temperatures by their burrowing and nocturnal habits.

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